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Cultural dietary stasis? Four decades on, Mahale chimpanzees still favour *Macrotermes*

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INTRODUCTION

Termite consumption by wild chimpanzees (*Pan troglodytes*) is widespread across Africa (McGrew 1992) but not universal (Fowler & Sommer 2007). When consumed, termites represent a valuable source of energy, fat, high-quality protein, minerals and vitamins (O'Malley & Power 2014). Frequency, acquisition techniques and choice of prey vary greatly among populations (Wondra *et al.* 2016). While some of these differences respond to the characteristics of the termite prey and ecological context, other aspects may more easily be attributed to social influences (Sanz *et al.* 2014). Of the 106 genera of soil-dwelling termites present in Afrotropical habitats (Krishna *et al.* 2013), only eight have been recorded as chimpanzee termite prey, with *Macrotermes* being the genus mostly eaten (Lesnik 2014).

Chimpanzees of Bilenge (B group) inhabiting the Mahale Mountains National Park in Tanzania were first reported to harvest *Macrotermes* with tools in 1975 (Nishida & Uehara 1980). Other termites such as *Odontotermes* and *Pseudacanthotermes spiniger* were more abundant but ignored (Collins & McGrew 1985).

Recent studies revealed that the B group has maintained their termite-fishing tradition for more than forty years (Pascual-Garrido 2017). However, if they continue to favour *Macrotermes* remains unknown. Here we document termite prey consumption by Mahale B group chimpanzees and compare with those reported decades ago (Collins & McGrew 1985). We discuss possible factors influencing this choice.

METHODS

The unhabituated chimpanzees (*Pan troglodytes schweinfurthii*) of B group live in Bilenge (6° 2' S, 29° 44' E; 772–1550 m elevation), the northwestern edge of the Mahale Mountains National Park in western Tanzania (Nishida & Uehara 1980). The dry season from mid-May to mid-October has virtually no rain. The rainy season generally has two peaks of rainfall in November and in March–April, with an average annual rainfall of about 1400 mm. Bilenge is mostly dominated by open grassy woodland, mainly *Brachystegia* (miombo), with vine tangles and forests only present in narrow strips along the valleys, and broad hilltops rising from the coastal plain (Collins & McGrew 1988). Termite-fishing though habitual, is highly seasonal, mainly taking place during the first half of the wet season (from October until at least February), which coincides with the annual and dispersal flights of the termites (Uehara 1982).

Three field seasons were conducted by APG assisted by one experienced Tanzanian field assistant (Nov 25th –

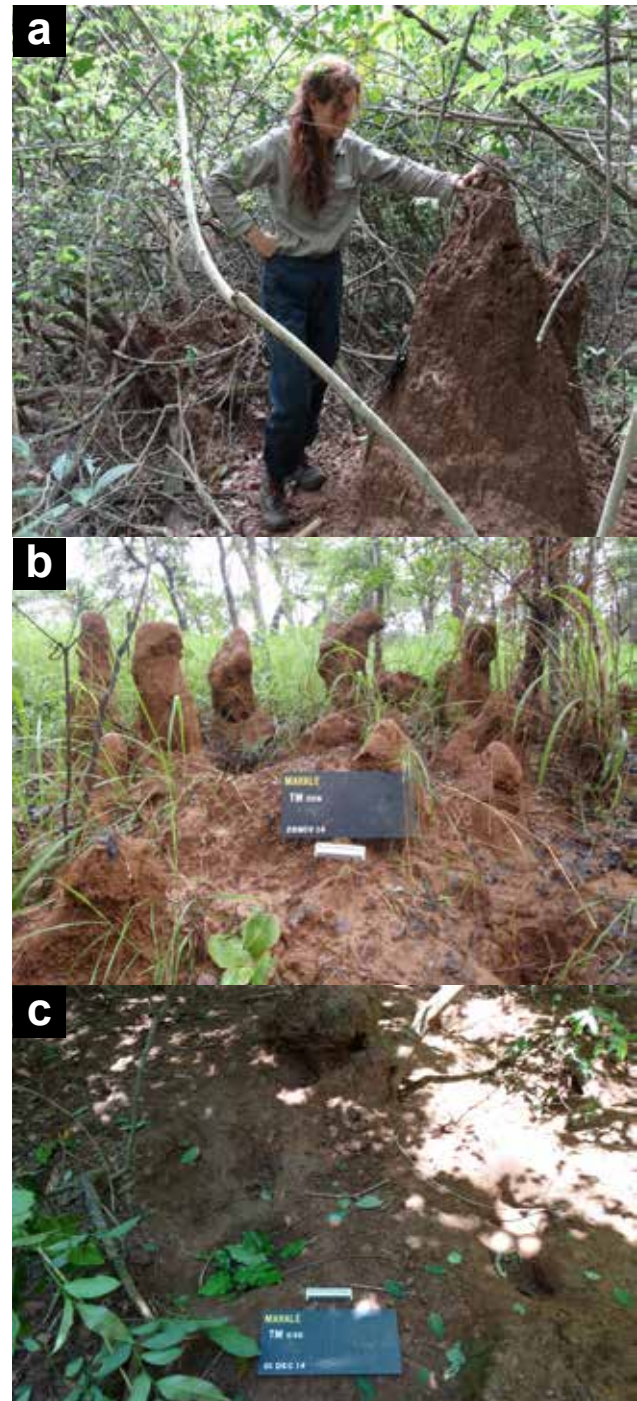


Figure 1. Termite genera in Bilenge. a) APG and a mound of *Pseudacanthotermes spiniger*; b) *Odontotermes*; c) *Macrotermes michaelseni* with recently abandoned termite fishing tools by chimpanzees (December 1st, 2014). Photo credits: Alejandra Pascual-Garrido.

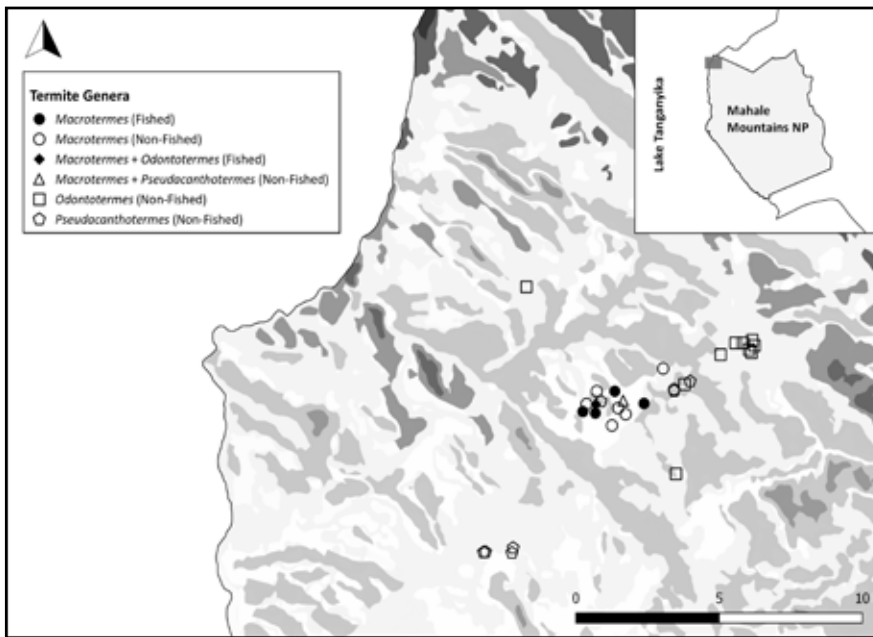


Figure 2. Map of the distribution of termite mounds surveyed at Bilege. Mounds fished by chimpanzees are shown in black. Map credits: Katarina Almeida-Warren.

Dec 14th, 2014; Oct 20th–Nov 8th, 2015; Nov 21st–Dec 8th, 2016). During reconnaissance surveys, APG searched for mounds which could potentially have been fished by chimpanzees within B's group range (Nishida & Uehara 1980). Mounds included broadly domed mounds, mounds with open ventilation holes and towers raised as chimney (Collins & McGrew 1985). Smaller mushroom-shaped mounds, typical of soil *Cubitermes*, were ignored given that they are not targeted with plant tools by chimpanzees (Collins & McGrew 1985; O'Malley & Power 2012) (though Bili-Uère chimpanzees use percussive technology to access them; Hicks *et al.* 2020). Data collected at each mound included GPS position and, based on archaeological methods (Pascual-Garrido 2018), evidence of each mound having been targeted by chimpanzees including: (a) tools, (b) plants sourced for tool material, (c) signs of damage (i.e. knuckleprints). For each mound, at least 10 termite specimens were collected, fixed in ethanol 80% and later identified by RS. Specimens collected included mostly soldiers. Workers and alates were collected when available.

RESULTS

A total of 36 mounds were sampled and identified. This included six genera and five species, with *Macrotermes*, *Pseudacanthotermes* and *Odontotermes* being the genera most represented (Figure 1). All mounds were occupied by a single resident species, except for four mounds where multiple occupants resided (Table 1). Soldiers were collected at all mounds, with alates only present at three *Macrotermes* mounds and at one *Odontotermes* mound. Only *Macrotermes michaelsoni* mounds showed signs of having been targeted by chimpanzees ($n=5$), one or multiple times (Pascual-Garrido 2017), and one also occupied with a second resident from the genus *Odontotermes* (Table 1; Figure 2). No evidence of chimpanzee predation was recorded for any other ter-

mite genera. Evidence of chimpanzee predation at mounds included tools ($n=1$), knuckleprints ($n=1$) and plants sourced for tool materials ($n=5$) (Pascual-Garrido 2017).

DISCUSSION

More than 40 years have passed and successive generations of Bilege chimpanzees continue to fish *Macrotermes* mounds while ignoring other termites also common in the area (Collins & McGrew 1985). *Macrotermes* are preyed on by more populations of chimpanzees than all other termite taxa, being the best-documented insect genus for ape use of elementary technology in extractive foraging (Lonsdorf 2005). Given the high nutritional value, fishability, greater mass and less noxious taste of these fungus-

farming termites compared to other genera (Collins & McGrew 1985; O'Malley & Power 2014), it is therefore not surprising that Bilege chimpanzees continue to fish them. But why do Bilege chimpanzees still ignore other genera such as *Odontotermes* and *Pseudacanthotermes*? The absence of *Odontotermes*' consumption, a genus not consumed by any wild chimpanzee population (except rehabilitated chimpanzees released in Rubondo Island in Tanzania; Moscovice *et al.* 2007), is not surprising: their distasteful defensive secretion makes them unpalatable for chimpanzees – and for humans too as corroborated by APG. More puzzling is the lack of ingestion of the highly nutritional and more abundant *P. spiniger* – a species habitually fished by the extinct neighbouring K group of Mahale (Uehara 1982) and by Issa chimpanzees living 114 km east of Bilege (Stewart & Piel 2014; Pascual-Garrido, unpublished data). It may be that Bilege apes fish *P. spiniger* later in the wet season (although Uehara's (1982) analysis from faecal samples suggests that they do not). That we failed to find any evidence of termite-fishing at these mounds, including plants used for tool making which, unlike tools, remain detectable for years (Pascual-Garrido 2018), makes this unlikely. If members of the B group eat alates (and soil) of *P. spiniger*, as neighbouring (extinct) K group and M group do without tools (Uehara 1982) (though see Takahata 1982 for use of tools by two immigrant chimpanzees from K group termite fishing at *P. spiniger* mounds), we would have missed it, as this can only be evidenced by direct observation of the apes (not possible at Bilege) or by faecal samples inspection (not included in this study). Still, at present we have no evidence for this – and certainly no signs at all that they fish them. The question therefore remains: Why do Bilege chimpanzees focus their termite-fishing exclusively on *Macrotermes*, as do Gombe chimpanzees, while ignoring *P. spiniger* whose major soldiers are high in energy, fat and protein and fished by other chimpanzee communities

Table 1. Termite family, subfamily, genera and species surveyed at Bilenge. Mounds targeted by chimpanzees appear in grey.

Termite mound	Family	Subfamily	Genera	Species
MTM023	Termitidae	Apicotermittinae	<i>Alyscotermes</i>	<i>kilimandjaricus</i>
MTM030	Termitidae	Macrotermittinae	<i>Macrotermes</i>	<i>michaelseni</i>
MTM050	Termitidae	Macrotermittinae	<i>Macrotermes</i>	<i>michaelseni</i>
MTM054	Termitidae	Macrotermittinae	<i>Macrotermes</i>	<i>michaelseni</i>
MTM051	Termitidae	Macrotermittinae	<i>Macrotermes</i>	<i>michaelseni</i>
MTM063	Termitidae	Macrotermittinae	<i>Macrotermes</i>	<i>michaelseni</i>
MTM063	Termitidae	Macrotermittinae	<i>Odontotermes</i>	
MTM018	Termitidae	Macrotermittinae	<i>Macrotermes</i>	<i>bellicosus</i> ; <i>michaelseni</i>
MTM033	Termitidae	Macrotermittinae	<i>Macrotermes</i>	<i>michaelseni</i>
MTM034	Termitidae	Macrotermittinae	<i>Macrotermes</i>	<i>michaelseni</i>
MTM055	Termitidae	Macrotermittinae	<i>Macrotermes</i>	<i>michaelseni</i>
MTM066	Termitidae	Macrotermittinae	<i>Macrotermes</i>	<i>michaelseni</i>
MTM036	Termitidae	Macrotermittinae	<i>Macrotermes</i>	<i>michaelseni</i>
MTM015	Termitidae	Macrotermittinae	<i>Macrotermes</i>	<i>michaelseni</i>
MTM017	Termitidae	Macrotermittinae	<i>Macrotermes</i>	<i>michaelseni</i> ; <i>lilljeborgi</i> ; <i>bellicosus</i>
MTM002	Termitidae	Macrotermittinae	<i>Microtermes</i>	
MTM021	Termitidae	Macrotermittinae	<i>Microtermes</i>	
MTM006	Termitidae	Macrotermittinae	<i>Odontotermes</i>	
MTM005	Termitidae	Macrotermittinae	<i>Odontotermes</i>	
MTM010	Termitidae	Macrotermittinae	<i>Odontotermes</i>	
MTM007	Termitidae	Macrotermittinae	<i>Odontotermes</i>	
MTM008	Termitidae	Macrotermittinae	<i>Odontotermes</i>	
MTM009	Termitidae	Macrotermittinae	<i>Odontotermes</i>	
MTM012	Termitidae	Macrotermittinae	<i>Odontotermes</i>	
MTM011	Termitidae	Macrotermittinae	<i>Odontotermes</i>	
MTM014	Termitidae	Macrotermittinae	<i>Odontotermes</i>	
MTM038	Termitidae	Macrotermittinae	<i>Odontotermes</i>	
MTM033	Termitidae	Macrotermittinae	<i>Pseudacanthotermes</i>	<i>spiniger</i>
MTM031	Termitidae	Macrotermittinae	<i>Pseudacanthotermes</i>	<i>spiniger</i>
MTM042	Termitidae	Macrotermittinae	<i>Pseudacanthotermes</i>	<i>spiniger</i>
MTM013	Termitidae	Macrotermittinae	<i>Pseudacanthotermes</i>	<i>spiniger</i>
MTM016	Termitidae	Macrotermittinae	<i>Pseudacanthotermes</i>	<i>spiniger</i>
MTM025	Termitidae	Macrotermittinae	<i>Pseudacanthotermes</i>	<i>spiniger</i>
MTM026	Termitidae	Macrotermittinae	<i>Pseudacanthotermes</i>	<i>spiniger</i>
MTM041	Termitidae	Macrotermittinae	<i>Pseudacanthotermes</i>	<i>spiniger</i>
MTM040	Termitidae	Macrotermittinae		
MTM024	Termitidae	Termitinae	<i>Microcerotermes</i>	
MTM004	Termitidae	Termitinae	<i>Microcerotermes</i>	

(Uehara 1982; O'Malley & Power 2012)?

One possibility could be that the density of *Pseudacanthotermes* at Bilenge has declined during the last decades and chimpanzees are selecting their prey subject to their availability. However, earlier studies indicate this is not the case (Collins & McGrew 1985), but that *P. spiniger* are ignored because of the soldier's smaller size and less value on a per-foraging-unit basis compared to *Macrotermes* (O'Malley & Power 2012). However, an extended termite fishing session on *P. spiniger* could still provide a nutritional meaningful yield of energy, fat and protein (O'Malley & Power 2012). Previous research indicates that techniques and type of tools used to harvest insects, including termites, is partly influenced by the behaviour of the species preyed upon (Schöning *et al.* 2008; Sanz *et al.* 2014). If *Macrotermes* are more fishable than *Pseudacanthotermes* (i.e. grip on the tool with greater force) remains to be tested.

Another possibility, perhaps more difficult to test, is that chimpanzees may be reluctant to try new food choices. Adult chimpanzees are conservative regarding their feeding habits, which can act as a selective force against a new food (Nishida *et al.* 1983). Still, they may consume a variety of human (crop) foods if available (McLennan &

Hockings 2014). Furthermore, captive and wild chimpanzees show a marked persistence for initially adopted strategies related to the acquisition of food, even when a strategy stops being successful (Gruber *et al.* 2009; Hrubesch *et al.* 2009). Conservatism can create within-group behavioural homogeneity, while Whiten *et al.* (2005) attributed it to conformity. Chimpanzees are highly selective regarding their insect prey choices (Webster *et al.* 2014). That some chimpanzee communities prey on termites, while others do not (Fowler & Sommer 2007), and that harvesting techniques differ between (and within) communities (McGrew 1983; Boesch *et al.* 2020), highlights the importance of investigating the mechanisms behind these differences. Social influences on food preferences are barely contemplated in current studies of chimpanzee culture (but see Hicks *et al.* 2020) – maybe because variation in feeding behaviour is more parsimoniously explained by ecological differences (Byrne 2007). However, Boesch *et al.* (2006) suggested that variation in feeding time relative to fruit availability may reflect cultural differences, while Hicks *et al.* (2020) found no association between insect availability and consumption. Likewise, Nishida *et al.* (1983) and Sakamaki *et al.* (2007) reported that two neighbouring groups at Mahale consume different food items, despite their equal availability in both areas. Similarly, neighbouring chimpanzee communities living in the Budongo Forest Reserve, Uganda, vary in their preference for red duiker (*Cephalophus natalensis*) consumption despite no difference in prey distribution (Hobaiter *et al.* 2017). Social learning plays a fundamental role in the acquisition of technological skills to harvest social insects, including food choices (Lonsdorf 2005; Schöning *et al.* 2008; O'Malley *et al.* 2012), and is key for the development and maintenance of cultural behaviours and traditions in primates (Schuppli & van Schaik 2019). Further research is warranted to establish if social learning in chimpanzees extends to their choice of termite prey.

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